Primary succession revisited

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INTRODUCTION

The aim of the symposium was to focus attention on the early stages of primary succession. It was hoped that, in reviewing the field of knowledge and concentrating on the major processes involved in primary succession, the symposium would, as well as identifying gaps in knowledge, identify more clearly than hitherto those features which distinguish primary from secondary succession.

In practice, gaps in knowledge appeared well before the symposium took place, as we tried to find speakers to cover the entire field of interest. Thus it proved quite impossible to find an aerobiologist to discuss long-distance dispersal of spores and other propagules in an ecological context. There also appeared to be an apparent lack of interest in the processes leading to the establishment of animal communities; Majer's (1989) recent volume *Animals in Primary Succession* throws little light on this. Dispersal has long been recognized by biologists as a key process, but one about which little is known for most species. Indeed, until recently, dispersal seemed commonly to be regarded by the major agencies which fund research as smacking of Victorian-era natural history. Interestingly, one consequence of current concerns about global climate change, and in the European Community about possible land-use changes (including the abandonment of agricultural land, which might result from reform of the Common Agricultural Policy), has been to persuade funding agencies of the need to support further work on processes of animal and plant dispersal and migration!

In what follows, we consider the symposium proceedings in the light of Bradshaw's analytical introduction, looking at succession: first, from the point of view of the plants and animals; second, from the point of view of their habitats; and third, considering species interactions and the development of succession. Interestingly, the steps which Bradshaw highlighted and discussed were all clearly identified early this century by Clements (1904, 1916).

ORGANISMS

Dispersal

Dispersal — the getting there — is clearly crucial to questions of colonization and

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succession. Smith's paper leads to the inference that there must be a large and widespread 'rain' of viable propagules of bryophytes in Antarctica. His studies have shown that ice and snowfields accumulate spores, and that one consequence of snowmelt is to ensure that recently exposed soils, even those remote from any established vegetation, contained often substantial pools of viable bryophyte propagules reflecting a diverse species assemblage. Similar rains of bryophyte propagules probably occur in other continents. Certainly, exposed soil in pots in glasshouses in temperate regions quickly becomes colonized by bryophytes, though these are usually ubiquitous pioneer species. However, in two experiments in upland Scotland to study soil change in which patches of mature birchwood were felled, the field layers killed by chemical herbicides, and the patches then planted with pre-established plants of *Calluna vulgaris* (heather), all the dozen or so mosses commonly associated with *Calluna* in nearby moorland were present after only 2–3 years (J. Miles, unpubl. data).

Little is known about the ability of most invertebrates to disperse over long distances, though the evidence correlating the spread of various European earthworm species across North America with the activities of freshwater anglers suggests that the dispersal powers of these are limited. Also in contrast to bryophytes, the dispersal powers of most flowering plants seem very limited. This poses few problems when sources of seeds or fruits are available in the vicinity. Thus, J. Miles (unpubl. data) examined the primary succession occurring on a 2-ha patch of calcareous mica-schist rock spoil which was deposited at the bottom of a hillside in Perthshire, Scotland, in the late 1950s during the construction of a long tunnel. The spoil was dumped at the conjunction of an expanse of *Calluna*-dominated moorland, a birchwood and a livestock farm. In 1974, the flora of the spoil heap contained most of the commonly occurring flowering plants of the adjacent moorland, woodland and reclaimed grasslands, and also a surprisingly large number of less common plants. The combination of the lime-rich and often finely crushed rock and an annual precipitation of about 1250 mm clearly provided a receptive substrate for what must have been a heavy local seed rain. However, relative isolation is probably more common. H. Ash (unpubl. data) has shown through experimental introductions that the characteristically poor floras of islands of industrial waste and spoil can be accounted for by their isolation from similar habitats where species grow which are adapted to the particular soil conditions. In this symposium, Whittaker & Bush's analysis of the re-colonization of the Krakatoa Islands after the 1883 eruption showed that even a century later the islands have very few tree species characteristic of inland areas, even though species characteristic of later stages of forest succession have continued to appear during the last 50 years. Most of the woodland cover is still provided by a few tree species characteristic of early successional stages. The effect of isolation in limiting succession on Krakatoa is also shown by the fact that most species colonizing are those commonly dispersed endozoically.

The studies of del Moral and his colleagues in the aftermath of the first Mount St Helens volcanic eruption in 1980 demonstrated yet again the crucial role of species accessibility in colonization and succession. Regrowth of vegetation at

Mount St Helens was quick only at sites with a species legacy. The conclusion is that the nature and direction of succession at Mount St Helens reflects the order of species arrival by dispersal, and nothing else. It would not be surprising if these stochastic effects persisted for decades. Indeed, studies such as those at Mount St Helens bear out the essential correctness of the views about the 'individualistic' nature of vegetation developed earlier this century independently by H. A. Gleason, F. Lenoble and L. G. Ramensky.

Establishment

Only Chapin's paper deals explicitly with establishment, and even he was forced in the main to make inferences from descriptive rather than experimental studies. Drawing largely on studies from north temperate and sub-Arctic regions, Chapin concluded that colonizers in primary succession commonly have traits which maximize dispersal but permit growth in dry, infertile sites. He concluded, like Whittaker & Bush, that woody species are important colonizers during primary succession, but also concluded that most have light, wind-dispersed seeds, which contrasts with the mainly endozoically dispersed tree flora that Whittaker & Bush found in Krakatoa. Species identified as common colonizers of primary substrates are characterized by low absolute growth rates, which contrasts with the generally high relative growth rates characteristic of pioneers in secondary successions. This highlights a crucial difference, indeed perhaps the most crucial difference, between primary and secondary successions, namely that the soils have a low content of organic matter and hence a low nitrogen content. The importance of acquiring a pool of nitrogen in soils on primary substrates to allow succession is stressed by Marrs & Bradshaw, and is also highlighted by Davy & Figueroa as a major determinant of establishment and success of strandline colonists.

Growth

Plants will only grow if they can acquire nutrients and water. Excluding the rather special cases of succession on beaches and sand dunes where the substrates may have been weathered and leached for millennia, primary successions commonly occur on relatively unweathered substrates. In these all the elements needed for plant nutrition may be present in abundance except for nitrogen and phosphorus, but especially the former. Most phosphorus comes directly from weathering of soil minerals, such as apatite. Its availability in primary successions is directly proportional to its abundance in the soil minerals. What is the origin of the nitrogen which accumulates during primary successions? Ammonia and nitric acid are now common atmospheric pollutants, though rates of deposition of these decline with increasing distance from source. Further, nearly all such inputs will be lost in run-off water unless an appreciable cover of plants is available to capture them. Wind-blown material should not be overlooked as a source of nitrogen; del Moral noted that organic matter fallout at Mount St Helens averaged $4\,mg\,m^{-2}\ day^{-1}$ during the growing season, and exceeded $10\,mg\,m^{-2}$

day^{-1} in places. Sprent noted that cyanobacteria are common on most sites, but that little is known about how much nitrogen they fix and how much of this is made available to subsequent stages in succession. However, fixation of nitrogen by cyanobacteria at maximum recorded levels of 15 kg N ha^{-1} year^{-1} could, together with other inputs, support some growth by flowering plants.

Both Gray and Chapin discuss characteristics of pioneer plants of primary succession. Such species do not show the sets of life-history traits usually thought to characterize pioneer plants of secondary succession. In contrast to secondary successions, the pioneer plants of primary successions are generally either long-lived iteroparous perennials or shrubs and trees. These are generally slow-growing, and commonly persist into the later stages of succession. Grubb (1986) commented on the remarkable variety of pioneer flowering-plant species found in primary successions, noting the common denomination that growth form and growth rate must match the capacity of the substratum to supply water and mineral nutrients.

Grubb (1986) also noted that the life-form of pioneers in primary succession recorded in different studies seemed to reflect physical differences in the nature of the substrata, with, for example, trees being common pioneers on rocky and bouldery substrata, iteroparous herbs on gravels and grasses on silty substrates. In an interesting case history Mazzoleni & Ricciardi describe how different plants colonizing the core of Vesuvius have selected different physical substrates.

However, any attempt to construct such general classifications is confounded by the tendency of plant species immigration to particular sites to be by particular mechanisms of dispersal. Thus it is not surprising that most species recorded on Krakatoa by Whittaker & Bush 100 years on in the succession appear to have arrived via the alimentary tracts of birds. It is similarly not surprising that del Moral found that most pioneers at Mount St Helens were either wind-dispersed or had survived the eruption. Yet the strandlines of the seashore and of gravel islands in fast-flowing rivers have colonists with a diversity of life histories; propagule mass is apparently irrelevant for dispersal by water.

There seem to be several reasons why trees and other woody shrubs are common pioneers in primary successions. Some genera such as *Salix*, *Populus* and *Betula* produce large numbers of small, light wind-dispersed propagules, which make them common pioneers in both primary and secondary successions. However, larger-seeded taxa, such as wind-dispersed *Pinus* and *Picea* spp. and bird-dispersed *Quercus* spp. are also common pioneers on landslips, mud flows and talus slopes. Grubb (1986) has suggested that many woody species of this type are good colonizers in primary succession because of their slower growth rates and hence lower nutrient requirements, while the relatively large seeds contain an appreciable initial source of nitrogen. Equally, their robust growth forms presumably allow them to survive in unstable rocky and bouldery areas where plants with softer tissues would be destroyed. Some trees also have remarkably extensive root systems; in stony substrates with intrinsically low water-holding capacities, it must be advantageous for a plant to have roots which can ramify down to the water-table or into a different substratum with a higher water content.

HABITAT

Initial characteristics

Grubb (1986), and in this volume del Moral and Mazzoleni & Ricciardi in particular, discuss how the physical characteristics of the substrate select for different groups of pioneers. Particularly coarse substrates develop a vegetation cover very slowly, perhaps mainly because of their very low water-holding capacity. Thus the west of Scotland has extensive raised beaches, 10 000 or more years old, which formed when the weight of the last glacial ice-cap had depressed the land relative to sea-level. Many of these beaches are of water-rounded boulders and are still largely devoid of vegetation, most notably on the Isle of Jura, apart from some epilithic lichens and mosses. Such substrates cannot of course weather into soil except on a geological time-scale, while the large spaces between boulders usually prevent the surface accumulation of appreciable amounts of airborne dust and organic matter.

A common characteristic of fine-grained primary substrates is their physical instability and hence proneness to movement by wind, water and frost action. Although records of the early stages of primary succession have usually only listed lichens, mosses and flowering plants, Wynn-Williams has clearly demonstrated the role of microbial crusts in stabilizing fine-textured primary substrates by binding mineral particles in a cyanobacterial and algal filament–mucigel matrix. Given the near ubiquity of cyanobacteria on primary sites (see Sprent), presumably because of their effective dispersal in the atmosphere, it seems highly probable that microbes may be the first, or among the first colonists, of all virgin substrates, and may initiate and facilitate plant succession.

Influence of autogenic factors

Walton and Wynn-Williams have both discussed the role of lower plants in primary successions. Almost all lower-plant taxa may have significant localized roles in accelerating the chemical weathering of minerals (so accelerating soil formation) and can be primary colonists of bare rocks and soils. Endolithic lichens can induce exfoliative weathering and hence promote the formation of fine-grained substrates, while terricolous lichens can stabilize the soil surface in areas prone to disruption by frost heaving. Mosses, like flowering plants, can scavenge and accumulate mineral particles, and so provide potential microsites and foci for establishment by flowering plants. The cryptoendolithic microbial communities described by Vestal may represent the self-renewing initial stages of primary successions which never proceed any further (unless the products of exfoliative weathering are taken into account) under existing climatic conditions.

The second stage at which autogenic factors seem to be crucial during primary successions is in establishing the store of organic nitrogen in the soil (and also of phosphorus in phosphorus-deficient substrates), which will allow sustained plant

growth during succession. Most studies and all reviews have noted the importance of symbiotic nitrogen fixation in the early stages of primary succession. The presence of *Alnus* and *Dryas* spp. in succession behind retreating glaciers has long been known, and other examples were quoted at the symposium. Generally the colonist symbiotic nitrogen fixers are legumes, but these rarely appear in the earliest stages of primary succession, apparently because these large-seeded species generally lack effective long-distance dispersal mechanisms. A notable exception to this is the rapid dispersal of certain legumes, e.g. *Lupinus nootkatensis*, along the banks of Arctic rivers.

Although the role of nitrogen-fixing flowering plants in promoting succession was originally largely speculative, there is now increasing evidence, some experimental, that this is indeed the case. Beyond nitrogen fixation, many plants exert a 'nurse' effect, as well as acting as filters for trapping wind-blown material. As a site supports a higher plant biomass, a soil structure develops. However, although past studies have demonstrated favourable chemical trends during soil development in primary successions, studies of the development of a soil structure favourable to root growth and of the development of a soil ecosystem have been largely ignored.

Influence of allogenic factors

As soon as a virgin substrate is exposed, it is subject to weathering of the component minerals, leaching away of elements (including leaching of toxic elements in man-made wastes) and to inputs of materials from the air. Apart from del Moral's observations, little was heard at the symposium about allogenic factors. However, except on toxic wastes, it is difficult to separate the effects of allogenic and autogenic factors, because propagules of bacteria, fungi, algae, lichens, mosses and flowering plants, as well as invertebrates appear from the outset. Their growth immediately begins to influence the physical and chemical nature of the substrates, and so confounds the effects of purely allogenic factors.

Continued succession

Species interactions presumably occur from the outset, but those such as grazing of algae or bryophytes by invertebrates are not obvious and have rarely been studied in primary successions, although invertebrate faecal material plays an important role in soil development. Most studies of succession have been by plant ecologists, so most reports of species interactions are those between different species of flowering plant. Competition has been rarely studied, but simple inhibition — because the first-come species monopolizes space — does seem to be important. Equally, there are many records and inferences of particular species acting as 'nurse' plants (see del Moral). In particular, it seems clear that symbiotic nitrogen fixation by legumes and other nodulated taxa does facilitate vegetation development.

More intriguing are reports about iteroparous perennials such as those in this volume by Gray, by van der Putten, and by Thomson *et al*. The persistence of species such as *Ammophila arenaria* and *Spartina anglica* during succession is fascinating, and the reports here indicate habitat-correlated phenotypic plasticity, and also somatic variation related to clonal age. However, van der Putten reports reduced biomass production by and clonal degeneration of *Ammophila arenaria* in stable sand dunes, apparently caused by pathogenic soil organisms, probably both nematodes and fungi. In this latter case, competition between different flowering plant species is not needed for the pioneer to decline.

CONCLUSIONS

The symposium showed that there are few differences between primary and secondary successions, but that those that do exist are crucial. Arguably the most important is that newly exposed or deposited primary substrates almost always lack a reserve of nitrogen (only a very few rocks, all sedimentary, contain significant amount of this), while phosphorus and water availability also commonly limit plant growth. Stands of woody vegetation can only develop once adequate plant-available nutrient reserves have accumulated in the soil (Marrs & Bradshaw).

The two other crucial factors which clearly differentiate primary from secondary successions are substrate instability and the lack of any bank of organisms and their propagules in the soil. The exposed soil of a newly ploughed arable field is a complex mineral–organic matrix which is hundreds or thousands of years in time from a primary substrate. In contrast, a primary substrate is mineral only, and lacks the various mucigels and organic fractions which bind mineral particles together and stabilize the soil surface, so inhibiting erosion and facilitating colonizations by plants and animals. The lack of a propagule bank — a 'memory' of a previous vegetation cover — means that the development of species assemblages during primary succession depends on the probabilistic processes of species dispersal. It thus minimizes the chances of any orderliness or repeatability of successions on similar substrates but occurring at different places and times.

These differences suggest interestingly that the annual development of vegetation on coastal strandlines, which has traditionally been described as primary succession, is perhaps better described as secondary succession. Two key criteria — the lack of an adequate nitrogen supply and of a bank of propagules — are usually not met (Davy & Figueroa).

All other main features differentiating primary from secondary successions — rates and variability of ecosystem development, and variability in the characteristics of the pioneering flowering-plant species — follow from these crucial differences in the nature of the substrate.

The symposium highlighted our relative ignorance on how, how far and how quickly most species are dispersed, and on their requirements for establishing individuals and populations. This is perhaps especially the case for invertebrates; although a good deal is known about their role in soil development (e.g. Majer

1989), very little is known about the conditions for establishing populations and assemblages. Precise definitions of species niches — of 'microsites' for plants — are needed as much as ever. Grubb's (1986) hypotheses about the variability in life-form of flowering-plant pioneers of primary succession badly need experimental testing. Yet experimental studies such as that by Harper *et al.* (1965), which showed the very fine scale of discrimination of soil surface microtopography by establishing seedlings of different *Plantago* spp., remain rare.

Perhaps the best recent insights into primary succession have come from the careful and detailed studies following the 1980 volcanic eruption at Mount St Helens (del Moral), and from the analytical and experimental studies in Antarctica by the British Antarctic Survey (Smith; Walton; Wynn-Williams) and now extended by the French to their sub-Antarctic islands. The Mount St Helens work has clearly shown the intrinsically stochastic nature of the dispersal of macro-organisms, and hence of the course of succession. The studies in Antarctica have shown in particular just how important micro-organisms are in stabilizing the surfaces of newly exposed substrates, and hence in facilitating subsequent succession. The two contrasting areas also highlight the difference between the effective long-distance dispersal in the atmosphere of bryophyte spores and of micro-organisms (which can also be inferred from Sprent's note on the apparent ubiquity of cyanobacteria in primary successions), and of the slow and difficult-to-predict dispersal of most species of flowering plant. There remains a great deal to be learnt about primary succession.

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